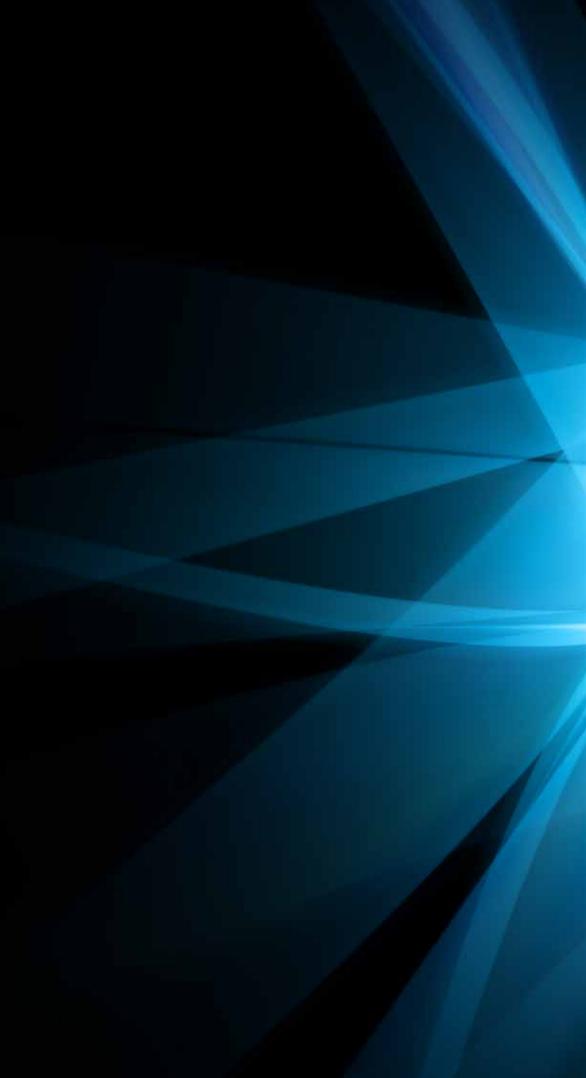
THE NOVO NORDISK PRIZE **PROFESSOR** POUL NISSEN



NOMINATION OF POUL NISSEN

The Novo Nordisk Foundation is awarding the 2017 Novo Nordisk Prize to Poul Nissen for his pioneering studies of the structure and function of membrane proteins.

Poul Nissen is 49 years old. He graduated with an MSc in chemistry within protein crystallography from Aarhus University in 1993. Subsequently, he carried out his PhD studies in molecular and structural biology at Aarhus University and obtained a PhD degree in 1997 for his work on protein and RNA factors involved in protein synthesis on the ribosome, with Associate Professor Jens Nyborg as the supervisor. Poul Nissen then moved to the laboratory of Thomas Steitz at Yale University. During his 3 years at Yale University, Poul Nissen played a pivotal role in determining the first ribosome structures and the fundamental mechanisms in protein synthesis – work that was later awarded the Nobel Prize in Chemistry in 2009 for Thomas A. Steitz together with Venkatraman Ramakrishnan and Ada Yonath. After his postdoctoral work at Yale, Poul Nissen returned to Aarhus University in 2000 as an Ole Rømer Fellow funded by the Danish Research Council. He started his own research at the Department of Molecular Biology and Genetics, focusing on eukaryotic ribosomes and membrane transport proteins. In 2002, he became an Associate Professor and, in 2006, Professor of Protein Biochemistry. In 2005, he received a 5-year Hallas Investigator fellowship from the Novo Nordisk Foundation. In 2007, he became the Director of the PUMPkin Centre (Centre for Membrane Pumps in Cells and Disease) funded by the Danish National Research Foundation. The Centre promotes interdisciplinary research on the structure and function of membrane transporters of the phosphorylated-type ATPase (P-type ATPase) family, including pathophysiological aspects and their potential as drug targets. In 2013, Poul Nissen was further appointed Director of the Danish Research Institute of Translational Neuroscience (DANDRITE), which is the Danish Node in Neuroscience (funded by the Lundbeck Foundation) of the Nordic EMBL Partnership for Molecular Medicine.

The function of every cell in our body depends on large differences in the concentrations of such ions as sodium, potassium and calcium inside and outside the cell. These concentration gradients across the cell membranes are maintained by P-type ATPases, which pump ions across the membrane, fuelled by the breakdown of energy-rich ATP molecules. Such ion gradients across cellular membranes potentiate, for example, the electrical signals of the nervous system and the activity of a wealth of transport systems in the cell for the uptake of such substances as nutrients, metabolites, hormones and neurotrans-

mitters and the excretion of waste products. The reaction cycle of P-type ATPases comprises several states that define a pump function, and the transitions between these are associated with conformational changes of the pump structure that reflect the chemical processes and the binding, translocation and release reactions carried out. The current understanding of the structural background of these processes largely depends on the results obtained by Poul Nissen and his group, and the process can now be followed as "molecular movies".

Throughout his whole career, Poul Nissen's scientific activities have been innovative both technically and conceptually. He has demonstrated outstanding ability to tackle structural biology at the cutting edge, which is technically very challenging, and in pursuit of profound biological insight, often with a translational dimension. He has succeeded in establishing his group in the front line of international research on membrane proteins.

In a series of articles published since 2004, Poul Nissen contributed to early breakthroughs in understanding of the structure and function of the sarco/endoplasmic reticulum calcium-ATPase (SERCA). His research group identified conformational changes preventing back flow before calcium is released on the other side of the membrane – a key aspect of pump function. A general mechanism was depicted of such occluded transition states of calcium transport and proton counter-transport coupled to phosphorylation and dephosphorylation, respectively. Later, crystal structures of the calcium-free state of SERCA were determined, describing a stimulatory role of ATP binding on the switch from outward- to inward-oriented states, reinitiating the pump for another cycle. Further, the mechanism of several inhibitors blocking SERCA function was identified.

Inspired by the success with SERCA, Poul Nissen embarked on new research on P-type ATPases and published three landmark articles in one issue of *Nature* in 2007 reporting the first atomic structure of Na+,K+-ATPase, also known as the sodium-potassium pump, another range of key structures of SERCA depicting the general transport mechanism of P-type ATPases, and the first structure of the plasma membrane proton pump. More recently, the first structures of copper-transporting pumps were also determined, which enabled molecular understanding of disease mutations associated with Menkes' and Wilson's disease, and of the related Zn²+-ATPase – structures that also provide new strategies for discovering new antibiotics and biotechnology associated with heavy-metal transport in plants and microorganisms.

Poul Nissen and his collaborators have also addressed the translational aspects of the structural findings and identified and explored P-type ATPases as potential drug targets. He has developed new experimental strategies for structural studies that facilitate drug discovery, and he participates in translational studies that investigate the function of disease mutations in cells and transgenic mice.

Along with many studies of P-type ATPases, his laboratory has also contributed to the fundamental understanding of the reuptake mechanism of neurotransmitters and amino acid transporters that are in fact potentiated by the Na⁺ gradient generated by the sodium-potassium pump. His current research very much reflects the need for deeper understanding of the network interactions of membrane proteins in biomembranes to address fundamental questions in cell biology.



Thus, the wealth of scientific results obtained by Poul Nissen through multidisciplinary approaches is outstanding. He has elucidated the general mechanistic basis for ion transport mediated by P-type ATPases and generated deep structurally based insight to investigate the basis of such diseases as nervous system disorders and mental disorders, cardiovascular diseases and cancer at the molecular level.

Poul Nissen is recognized globally as an international leader in his field and a leading exponent of modern integrated structural biology. He has an impressive scientific output of more than 140 original studies, many published in high-impact journals such as *Nature, Science* and *Proceedings of the National Academy of Sciences of the United States of America*. He has also authored several review articles in his field, and many of his reviews and original articles are highly cited.

He has participated in many collaborations with highly esteemed researchers both in Denmark and elsewhere. Poul Nissen has been honoured with several national and international prizes and awards, most recently the Gregori Aminoff Prize of the Royal Swedish Academy of Sciences. Further, he has attracted considerable external funding such as from the European Research Council. He has shown great leadership and mentored a cadre of excellent scientists and numerous young researchers and PhD students that are now continuing their own research at globally leading research institutions and companies, and he has attracted numerous researchers to work in Denmark.

In summary, the Novo Nordisk Prize Committee finds that Poul Nissen is a worthy recipient of the 2017 Novo Nordisk Prize based on his systematic, comprehensive, groundbreaking and highly esteemed international research on the structure and function of P-type ATPase ion pumps.

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CURRICULUM VITAE

POUL NISSEN

PROFESSOR BORN 11 MAY 1967, AUGUSTENBORG, DENMARK

Director, Danish Research Institute of Translational Neuroscience (DANDRITE), Aarhus University, Denmark (h-index 50, Web of Science)
Elected fellow of the Danish Academy of Natural Sciences
Director, Centre for Membrane Pumps in Cells and Disease (PUMPkin Centre), Danish National Research Foundation
Elected fellow the Royal Danish Academy for Science and Letters
Elected fellow European Molecular Biology Organisation (EMBO)
Ole Rømer research fellow, Aarhus University
Postdoctoral Fellow, Yale University, United States
PhD Prize (Gold Medal), Danish Academy of Natural Sciences
PhD in molecular biology, Aarhus University
MSc in chemistry, Aarhus University

All life is based on structures. And knowing these structures is the foundation for understanding life. Poul Nissen, the recipient of the 2017 Novo Nordisk Prize, has studied the basic structures that create coherence in living organisms his whole life.

STRUCTURE IS THE KEY

BY MORTEN BUSCH

Understanding life is all about breaking things into bits and pieces. Already as a child, Poul Nissen often took objects apart to understand how they work. As a scientist, he has continued to do this and he has determined some of the most complicated structures of biological molecules and system such as ribosomes and ion pumps.

"You cannot understand how a bike works until you actually see it and watch someone riding it. Then you actually start understanding it. Similarly, with X-ray crystallography, we need to take many different snapshots to realize how things work," Poul Nissen, Professor at the Department of Molecular Biology and Genetics at Aarhus University, explains.

Poul Nissen has spent most of his career applying and refining X-ray techniques so that they can be used to determine some of the most basic structures in biology to answer questions about life. He hopes that understanding the structures and mechanisms of biological molecules ultimately will help to develop new biotechnology, and to understand and cure disease. A good example is the structure of the crucial sodium and potassium pump (Na-K pump) – a structure Poul Nissen's team solved in 2007.

"The Na-K pump generates steep ion gradients that enable many other substances to be transported in and out of cells. So when a pump does not work well – if it has a mutation, for example, it can cause a central nervous system disease. Understanding how the pump works will tell us where it goes wrong in the process of the function to which it is coupled. And ultimately help in finding a cure for a disease."

FARMERS, PRIESTS AND BOTANISTS

Poul Nissen grew up on a large farm in Augustenborg on the island of Als. This upbringing affected his future in many ways, especially because of the mix of people around him. His immediate family included priests, botanists, teachers and, not least, farmers. As a result, he therefore got philosophy, science and especially nature under his skin at a young age.

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"I think growing up on a farm is like growing up in a huge laboratory. Being together all the time with nature, since it is both around us and on the farm. Looking at how you interact with nature influenced me a lot. And it made me curious to understand the mechanism of life. Why do things grow as they do? Why do things react as they react? What are the inner workings of life? That influenced me a lot."

For Poul Nissen, viewing things at a distance has never been enough. He always wants to dig under the surface to see what is hidden.

"I have always been very interested in understanding things in detail, so as a child I always wanted to know what was inside things and how they worked. I think that was what drove me towards research – to understand the actual mechanisms of things and answer the questions we have."

STRUCTURING A WILD SCIENTIST

For Poul Nissen, trying to understand the processes of life was a natural development. When he finished school and was considering what to do, the combination of chemistry and biochemistry appealed to him. Here he could try to understand how the molecules in cells work.

Although the inspiration to study biochemistry originated from Poul Nissen's upbringing, the inspiration for what kind of research to pursue came from somewhere completely different – his studies abroad in Spain, funded through an Erasmus Mundus scholarship. The stay in Madrid was crucial to his career in many ways.

"During my early studies, I had not been very focused but used my time to enjoy life. And I did that too while I was in Madrid, but the stay was also my first experience with my own experimental project, and it greatly inspired me to continue and later get a PhD degree. But because of my lack of study focus, I would almost certainly never have had the chance had it been nowadays."

One of the pioneers of X-ray protein crystallography in Denmark – Jens Nyborg – gave Poul Nissen the opportunity to do a PhD in his group, and he would soon be structuring the life of the young scientist.

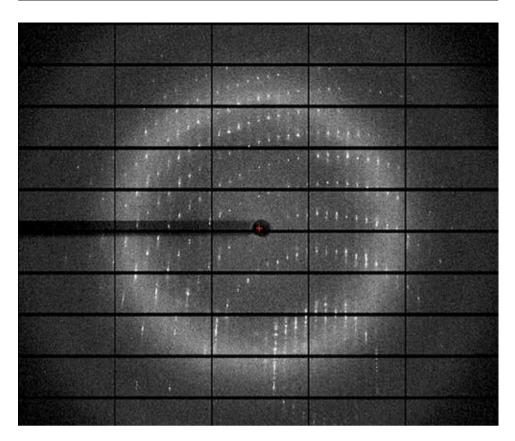
"I will never forget having the first classes with him and watching molecules with electron density maps and seeing directly how molecules build up three-dimensional structures and functionalities. Seeing water molecules interacting with a protein surface and really defining biology at a very elemental level was very inspiring to me."

A PERFECT MATCH

The partnership with Jens Nyborg proved to be a good match. Great results were created rapidly. During his MSc studies, he was deeply involved in determining the first structure of the translation elongation factor EF-Tu (elongation factor thermo unstable) in its active form, an essential protein factor of protein synthesis and probably the ancestor of the G-protein family.

In 1995, already halfway through his PhD programme, Poul Nissen had another major scientific breakthrough as the first author of an article in *Science* in which he had determined the crystal structure of EF-Tu with transfer RNA (tRNA).

That result was a stunning and rather unique example of molecular mimicry, since the structure turned out to have the same overall



DIFFRACTION PATTERNS

Diffraction refers to the phenomena that occurs when a wave encounters an obstacle. Diffraction occurs with all waves, including water waves, soundwaves and X-rays. As atoms cause a beam of incident X-rays to diffract, X-rays can be used to determine the atomic and molecular structure when they are arranged in crystals. By measuring the intensities and angles of diffracted beams, a crystallographer can create a three-dimensional picture of the density of electrons within a protein crystal.

Courtesy of Jacob. L. Andersen and Poul Nissen

shape as another translation elongation factor, EF-G, also known as the ribosomal translocase. The identification of the structure of the large complex was a scientific bestseller.

"It created quite a stir. A bunch of Danes had ended up in the world's most prestigious scientific journal. This was far from normal at that time. Danish media produced features and wrote articles about our research. This was also not standard at the time and was perhaps looked down upon by some. In general, researchers did not appear in the media at that time to talk about their research."

However, the research did give Poul Nissen a taste of success and faith in his abilities, and this enabled him to get a postdoctoral fellowship to work with Tom Steitz at Yale University in the United States. His X-ray crystallography project was also great: determining the structure of one of the most central structures of cells – the ribosome.

SIMPLE PRINCIPLES AND GREAT CONTEXTS

The task of mapping the structure of the ribosome was the starting-point and inspiration for many of Poul Nissen's later research projects. The ribosome is responsible for a central feature of all cells: to translate the genetic code and synthesize proteins that create structures and catalyse the processes of our cells.

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"Tom Steitz was a master of identifying challenging projects at the right time and completing them. He possessed the ability to unite what is exciting with what is also realistic. He always knew how to make research exciting and at the same time highly relevant – and this was also extremely motivating for young researchers."

After the results for partial structures had been published in the leading journals *Cell* and *Nature*, the Yale team published the first complete structure of the large ribosomal subunit in 2000 as two major articles in *Science*. The news hit newspapers and television broadcasts all over the world.

Both projects had taught Poul Nissen that good research must always be both exciting and innovative.

"If you find the science exciting and communicate honestly and clearly your enthusiasm for its importance and relevance, others tend to find it exciting too. I think what drives us in science is our curiosity for things we do not understand and that we want or even need to understand. When you approach such questions, and do it wisely, it will always be good science. And suddenly we obtain insights, mechanisms or applications that we maybe had not even thought of."

Tom Steitz in 2009 got the Nobel Prize in Chemistry for studies of the structure and function of the ribosome. Three of the key articles qualifying his nomination for the Prize were published with Poul Nissen.

BACK TO AARHUS

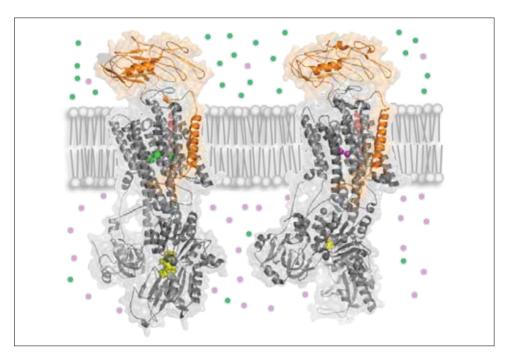
A highly successful adventure in the United States included also a medical student research scholarship at Yale Medical School for his wife, Marie Louise, and the birth of their two children, Sigrid and Kristian. Now it was time for Poul Nissen and the family of four to return to Aarhus. It was also the time for Poul Nissen to find new major biological challenges to solve through his own independent research.

In 2000, he received an Ole Rømer Fellowship from the Danish Research Council to work at the Department of Molecular and Structural Biology at Aarhus University, a department now named Molecular Biology and Genetics.

"When protein X-ray crystallography was initiated, it was a science on its own to develop the methods and to figure out how to actually determine the structures of gigantic molecules as proteins. It was largely defined by which proteins could be crystallized and would diffract well at all. By 2000, protein X-ray crystallography had become integrated into molecular biology and driven by the biological questions we wanted to pursue."

Above all, scientists had to learn how to make the crystals that were needed to determine the structure of proteins. A particular challenge was membrane proteins, which include receptors and transporters and have crucial functions in cells. The proteins within the membrane exist in a lipid phase but are also exposed to the aqueous phases inside and outside the cell.

"When you take membrane proteins out of their natural, fat-rich environment, they become unstable, and making crystals is therefore very difficult. However, by 2000, research had identified useful strategies to overcome such obstacles, and although they were still highly risky projects, it had become possible to define strategies for structure



Two different structures of the sodium-potassium pump placed in a schematic cell membrane. On the left side, the pump binds 3 Na⁺ ions (shown as green spheres in the middle), while on the right side it binds 2 K⁺ ions (purple spheres). Large conformational changes associated with the transport mechanism are clearly seen by comparing these two structures associated with Na⁺ extrusion and K⁺ import, respectively. The pump consists of three protein chains called alpha (grey), beta (orange) and gamma (red, barely visible in the back) encompassing a total of about 25,000 atoms (Morth et al. 2007, *Nature* and Nyblom, Poulsen, Gourdon et al. 2013, *Science*).

Courtesy of Jacob. L. Andersen and Poul Nissen

determination of membrane proteins. One of these was the calcium pump, a project to be performed in collaboration with Jesper Vuust Møller at Aarhus University."

A NATURE TRILOGY

Things, however, did not go quite as planned. Poul Nissen was just about to leave for Denmark when researchers from the University of Tokyo published an initial structure of the calcium pump. However, one structure is not enough to understand the transport mechanism of a pump and the structure of several other ion pumps still needed to be determined. So Poul Nissen decided to continue.

"With X-ray crystallography, you need to take many different snapshots to understand how things work and really understand the mechanisms. As examples for an ion pump: when it binds ions on one side, when it includes them in the membrane and when it releases them on the other side. Determining the structure of the protein during these individual steps tells us how the molecule work."

Fortunately, Poul Nissen had made the right decision by continuing. In 2004, he published his first articles on new structures and insights into the mechanism of the calcium pump, including two articles in *Science*, and in 2005 he received a Hallas-Møller Investigator Fellowship from the Novo Nordisk Foundation of DKK 5.2 million.

In 2007, he made a sweep with his colleagues and collaborators. With three articles in a single issue of *Nature* as well as the cover page, Poul

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Nissen had effectively put Aarhus University and Danish research on the world map.

One of the articles was about yet additional and decisive structures relating to the transport function of the calcium pump, another on the first structure of a proton pump and the third one described the first structure of the Na-K pump. The pump that Danish Nobel Prize winner Jens Christian Skou – also from the Aarhus University – had described exactly 50 years earlier.

"Understanding pumps tells you something about how cells control their environment. How do they solve the challenge of maintaining high and low concentrations of different ions inside and outside the cell? Maintaining these concentration gradients is absolutely fundamental to life, since it is responsible for driving the transport of other substances through the cell membrane and for cell signalling systems."

IN SKOU'S FOOTSTEPS

The three *Nature* articles also marked the beginning of a major research effort in biological membranes, since Poul Nissen earlier that year had become the Director of the Centre for Membrane Pumps in Cells and Disease (PUMPkin Centre), a centre of excellence to be funded for the maximum 10 years by the Danish National Research Foundation. The Centre aimed at investigating the function and mechanisms of P-type ATPases – the membrane protein family that includes the well-known ion pumps, but also lipid transporters and orphan transporters: that is, transporters with unknown function. As a truly innovative aspect of the Centre, the aim was also to translate insight into the mechanisms and functions of pumps to new strategies for application in medicine, drug discovery and biotechnology.

Because the pumps are central to the function of cells, cancer cells can be made to commit suicide by pharmaceutically interfering with the function of the pumps. PUMPkin researchers, through knowledge of the pump structure and function, could predict which types of substances could potentially affect the pumps.

"The most innovative aspect about the PUMPkin Centre was interdisciplinarity. We encompassed experts in such key disciplines as structural biology, biochemistry, cell biology, electrophysiology transgenic models and bioinformatics under the same roof. This enabled findings to be illuminated rapidly from different angles and to determine if we could find potential new drugs to fight disease causing mutations or create other societal benefits."

In 2013 alone, the PUMPkin researchers published 31 peer-reviewed articles – three of them in *Nature, Nature Genetics* and *Science*. The articles ranged from molecular medicine-oriented research on mutations in the Na-K pump in adrenal tumours, to new structures of the Na-K pump and the calcium pump.

INTO THE MIND

The work on the Na-K pump structure and mechanism gave the researchers unprecedented insight into their role in the health and disease of the brain. It also provided the necessary inspiration for Poul Nissen's step into the next major research centre, the Danish Research Institute of Translational Neuroscience (DANDRITE), which Poul Nissen started in 2013 together with colleagues at Aarhus University and the Nordic-EMBL Partnership for Molecular Medicine based on an open call by the Lundbeck Foundation.

"The function of pumps is crucial for the interactions between neurons in the brain. In fact, the brain uses about 40–70% of its total energy consumption to run the ion pumps. Defective pumps in brain cells can cause severe neurological conditions, such as migraine, dystonia, epileptic seizures and paralysis as well as mental co-manifestations. This highlights how deeply pump function is integrated into brain function. The brain was an obvious next step for our research."

DANDRITE focuses on how molecular mechanisms link to cellular interaction networks in the brain circuitry, and how these mechanisms are affected in diseases of the brain. Further, the researchers hope to develop new strategies in diagnostics, therapeutics and clinical practice for brain diseases.

"Brain function is about different areas of the brain communicating and solving tasks, which again controls behaviour. This gigantic network of interacting cells builds on the concerted action of thousands of macromolecules: intracellular and membrane proteins. How they work together and make these sophisticated functions – such as our consciousness – will be the next frontier of molecular and structural biology."

THE POWER OF SCIENCE

DANDRITE follows the EMBL model, where five young group leaders from around the globe in leading laboratories in Basel, Cold Spring Harbour, San Diego, Vienna and Stockholm were recruited to establish a thriving, cutting-edge research environment.

"The concept of EMBL is not only cutting-edge research but also creating tomorrow's research leaders. We recruit young group leaders, knowing that they will not stay with DANDRITE for life but for a maximum of 9 years. It is considered a success when they move on to positions as research leader somewhere else, with a cutting-edge research programme developed here."

The goal of the EMBL model is to stimulate original and innovative research. This is yet another aspect of the research, on which Poul Nissen has focused throughout his career, and will also be a trademark for DANDRITE.

"An extremely important aspect of research is to train new generations of researchers. I think one of the best and most stimulating ways of training new generations of researchers is through basic research with open questions that require creative thinking. At the same time, it is important to maintain a healthy balance between basic and applied research. It is a big mistake to think that all young scientists trained in basic research should continue doing basic research. Far from it."

Poul Nissen therefore thinks that academic research has a very important role of combining and exposing different research aims – both new, long-term basic research objectives and applied research aims. Applications such as drug discovery, clinical and industry collaborations and spin-out activities will therefore also be encouraged in DANDRITE, but Poul Nissen is careful not to try to plan or predict the possible applications.

"It's obvious that people in the Stone Age did not have a plan that we should drive electric cars and live in houses with central heating. The developments just came out of unplanned discoveries followed up by applied research. This is powerful and why science is so important. It will always open new avenues for us and help us discover new frontiers."



THE NOVO NORDISK PRIZE COMMITTEE

The Novo Nordisk Prize, which was first conferred in 1963, is awarded to recognize unique medical research or other research contributions that benefit medical science. The Prize is awarded for a predominantly Danish contribution.

The Prize is awarded annually and is accompanied by DKK 3 million – of which DKK 500,000 is a personal award, with the remaining amount as an allowance for research purposes within the Prize recipient's field of expertise. The Prize may not be awarded to members of the Board of the Novo Nordisk Foundation or members of committees or to members of boards, directors or employees of the Novo Group. The Novo Nordisk Prize Committee awards the Prize based on suggestions from past Prize recipients or members of the Prize Committee.

The members of the Novo Nordisk Prize Committee are appointed by the Novo Nordisk Foundation's Board of Directors, and the Committee currently comprises 7 members:

- Jan Fahrenkrug, professor, chair
- Jørgen Frøkiær, professor
- Lars Fugger, professor
- Marja Jäättelä, professor
- Mads Melbye, professor
- Thue W. Schwartz, professor
- Birgitte Nauntofte, CEO, Novo Nordisk Foundation

At the Committee meetings, the nominated candidates are thoroughly discussed with regard to their research contribution and impact, and a comprehensive bibliometric report is produced. A limited number of candidates are then selected for thorough international peer review. Based on the international peer reviews, the Committee reaches a decision about the year's Prize recipient.

The Foundation's collaborating partners and the Prize recipient's guests attend the award ceremony in the spring, where the recipient introduces his or her research for 15–20 minutes. In addition, in celebration of the award, the recipient gives a 1-hour lecture at his or her workplace. Before the end of the year, the recipient and the Foundation arrange an international symposium within the recipient's scientific field.

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